

DISTRIBUTION PATTERNS OF SPONGES AND CORALS DOWN TO 107 M OFF NORTH JAMAICA

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Sixty species of sponges (23 new) were collected from the deep fore-reef (60-107m depth) off the North Jamaican Discovery Bay area using trimix diving. Comparison with the shallow water sponge fauna shows only 15% of shallow water sponges extend down to the deep fore-reef and 60% of deep fore-reef sponges are not found in shallow water. Mapping sponge and coral distributions around Discovery Bay to 40m depth revealed a database of 102 sites with a surveyed area of 1659m². Multivariate analysis of this database recognizes three large scale habitats: Reef-surfaces, lagoon, and undersides of platy corals. Separate analyses of subsets indicate internal differences within habitats. Benthic colonization on reef-surfaces are continuous along depth and inclination gradients, except around river mouths. Within lagoon habitats there are subhabitats: blue hole, *Thalassia* seagrass-beds, ridges with freshwater outflow and protected (eastern) backreef. Zonation of Jamaican reefs appears to have changed over 34 years in comparison to data of Goreau (1959). □ *Porifera, distribution patterns, depth zonation, habitat specialisation, Jamaica, coral reefs.*

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Zonation patterns of corals have been studied by several workers (Goreau, 1959; Geister, 1977). Several authors (Liddell & Ohlhorst, 1987; Rützler, 1971, 1974, Wilkinson & Cheshire, 1989; Wilkinson & Evans, 1989; Zea, 1993) mentioned the importance of sponges in coral reefs, only few (Alcolado, 1990; Alvarez et. al., 1990; Diaz et. al., 1990; Schmahl, 1990) have attempted to describe the zonation of sponges, probably due to taxonomic difficulties within this group (Rützler, 1987; Böger, 1988, Van Soest, 1991). The first extensive study of Jamaican sponges was attempted by Hechtel (1965). He investigated the area of Port Royal on the Jamaican south coast, recording 57 species and listing the common species in each of his ten collecting areas. Few details were given on the nature of these localities but he did mention that a considerable number were restricted to certain habitats. This is surprising considering that his survey extended down to only 6.1m (20ft) depth. This implies sponges may have strong zonation patterns.

Previous studies on zonation of coral reefs recognized more intuitive morphological differences in reefs and based their zonation only in part on the sessile organisms occurring there, mainly on scleractinian corals. Geister (1977)

wrote that in Caribbean reefs there was a "distinct coral zonation controlled by exposure to wave activity. Based on this zonation, six basic reef types can be distinguished, ..." But he admitted that "Influence of factors other than wave exposure, however, may considerably disturb the regular zonation pattern". Geister (1983) gave an excellent overview about reef definitions, classifications and geological aspects of recent reefs, but worked on relatively large temporal and spatial scales.

The present paper is based on mapping of species from selected sites and subsequent multivariate analyses. The mapping of sponges and corals provides an estimate of the importance of sponges compared to corals. The aim of this study is to determine if similar species communities occur on different sites investigated, and if these similarities can be explained by environmental factors.

MATERIALS AND METHODS

Thirteen trimix dives to depths between 60-107m were undertaken in Discovery Bay, Jamaica in May-June 1993 and June-July 1996, to collect and photograph sponges of the deep fore-reef.

TABLE 1. Outline of classification undertaken on data, using methods proposed by Wildi (1989).

Program	Action	Comment
TRAFOA (PPS)	Histogram equation (Fischer, 1994)	Compensation of the extreme right-skewed distribution of population data.
	Species selection by variance.	Only species with highest variance, with total variance of 95% of the whole data set, were selected to reduce the data set and to reduce "noise".
INIT (MULVA)	Transform attribute vectors to unit length.	Avoid undesired effects caused by unequal species variance
RESE (MULVA)	Calculate similarity matrix using similarity ratio.	Recommended for sites
CLTR (MULVA)	Classify sites with minimum variance classification.	Minimizes in-group variance and maximizes between-group variance
INIT (MULVA)	Transform site vectors to unit length.	Avoid undesired effects caused by unequal species numbers in sites
RESE (MULVA)	Calculate dissimilarity matrix using chord distance.	Recommended for species
CLTR (MULVA)	Classify species with minimum variance classification.	Minimizes in-group variance and maximizes between-group variance
DIAN (MULVA)	Analysis of variance (Jancey's F-rank see Wildi, 1990) with $F > 2.6$ ($\alpha = 1\%$)	Select only significantly different species
INIT (MULVA)	Transform data for correspondence analysis	Required for correspondence analysis
RESE (MULVA)	Calculate similarity matrix using non centered cross product	Is required for correspondence analysis
PCAB (MULVA)	Compute correspondence analysis	Normal version chosen
AOCL (MULVA)	Analysis of concentration	Ordination of species and site- groups to get meaningful sequences
EDGR (MULVA)	Rearrange groups internally according to correspondence analysis	Obtain meaningful within group sequence of species and sites
TABS (MULVA)	Display the ordered table	-

Between January-July 1993 coral reefs in the Discovery Bay area, from the mouth of the Rio Bueno in the west to the mouth of the Pear Tree River in the east, were mapped using SCUBA, using the method described by Braun-Blanquet (1964). This method, originally developed for botanical surveys, was used to estimate the abundance and percentage cover of sponge and coral species in different habitats of reefs. Site surface area was measured with a plastic tape measure, and percentage cover of sessile species was estimated using the following procedure: r=one individual specimen in the site surveyed; +=cover below 1%; l=cover below 5%; m=cover below 5%, but species abundant; a=cover 5-15%; b=cover 15-25%; 3=cover 25-50%; 4=cover 50-75%; 5=cover 75-100%.

Large differences in size in both habitat and species occurrence (especially within sponges) necessitated adjustment of the size of sites according to prevailing conditions. Some habitats (e.g. undersides of platy corals), were very limited in their extent, whereas habitats like *Thalassia* sea-grass beds inside the lagoon, in shallow water, were far more extensive. Another factor limiting size of sites was decreasing bottom-time with increased depth. Evaluation of

these data was performed using MULVA (Wildi & Orlóci, 1990), CANOCO (ter Braak, 1988, 1990) and PPS (Fischer, 1994).

Classification of data was made using the standard strategy for the analysis of phytosociological data, suggested by Wildi (1989) with some modifications. Table 1 summarizes the analysis path.

Ordination was performed with CANOCO (ter Braak 1988, 1990) based on redundancy analysis (RDA), analyzing the influence of environmental factors on the fauna and providing graphical representation of the data. CANOCO offers two methods for canonical analysis: RDA and canonical correspondence analysis (CCA). CCA is preferable if the data set demonstrates large β -diversity, (i.e. if it contains several very different habitat types with very few or no species occurring in all of these types). RDA, in contrast, is applicable for small β -diversity. Our sites were recorded from a geographically small area from similar habitats. Several species were found in most of these habitats. Consequently, RDA is the preferable method for our data set. Graphical representation of canonical ordination (RDA) depicts similarity in distance between sites based on their faunistic and ecological affinities. Metric

TABLE 2: Jamaican corals and sponges. Columns represent site groups. The numbers are percentage frequency of the species. Site groups and species are arranged according to classification and correspondence analysis. Species groups (Sp. Gps) are indicated for each species. Site-groups are sites with similar species; co-occurring species are species-groups. 85 originally mapped species underwent an analysis of variance (see Table 1). The displayed 36 species have significantly different occurrence. Species not displayed are either very rare or run through all or most sites.

	Site-Group		4	3	8	5	6	7	10	9	1	2
	Number Of Sites		3	3	12	9	22	13	22	9	3	6
	Mean Number Of Species		3	5	12	12	16	12	10	9	2	4
ID	SPECIES NAME	Sp. Gps										
40	<i>Plakortis simplex</i> (olive)	17		100	17		5					
12	<i>Clathrina primordialis</i>	17	33	100								
9	Unidentified demosponge	17		100								
85	<i>Sylaster roseus</i>	16	100			22		23				
55	olive incrusting	16	100	67								
84	<i>Helioseris cucullata</i>	10			33				5			
28	<i>Agelas sceprrun</i>	10		67	75		9					
11	<i>Ectyoplasia ferox</i>	9			50		32		9	11		
61	<i>Agaricia agaricites</i> var. <i>unifaciata</i>	11			92	56	59	31	55	11		
60	<i>Montastrea cavernosa</i>	11			67	11	50	38	32	22		
58	<i>Acropora cervicornis</i>	4			8	22	55	15	14			
25	<i>Agelas dispar</i>	3			25	89	82	38	50	11		
71	<i>Siderastrea radians</i>	3			8	33	73	31	45	11		
41	<i>Erylus formosus</i>	2			17	11	55	8		11		
81	<i>Millepora complanata</i>	19			8	11	14	85	9	11		
57	<i>Acropora palmata</i>	19						23				
35	<i>Iotrochota birotulata</i>	6			8		45	15	55	33		
10	<i>Niphates erecta</i>	6				11	27	8	45	44		
13	<i>Ircinia strobilina</i>	6			17	67	77	31	36	33		
69	<i>Diploria clivosa</i>	20						46	9	44		
43	<i>Anthosignella varians</i> var. <i>incrustans</i>	20			25		18	54	27	56		
44	<i>Chondrilla nucula</i>	20				33	5	54	5	44		
1	<i>Neofibularia nolitangere</i>	5					9	8	45	22		
79	<i>Porites furcata</i>	1			17	89	82	69	23	44		17
78	<i>Porites astreoides</i>	1			58	100	77	92	32	56	33	
62	<i>Agaricia agaricites</i> var. <i>massiva</i>	1			33	44	64	54	14	22		
59	<i>Montastrea annularis</i>	1			83	78	100	92	59	22		
82	<i>Millepora alvicornis</i>	1			17	56	59	38	18	11		
15	<i>Aiolocroia crassa</i>	1			42	44	82	31	32	11		
46	<i>Aka coralliphaga</i>	1			8	78	9	38	9			
68	<i>Diploria labyrinthiformis</i>	1					32	54				
72	<i>Siderastrea siderea</i>	12			17		9	8	9	78		
49	<i>Xestospongia carbonaria</i>	18									100	67
54	<i>Haliclona coerulea</i>	18										50
48	<i>Myrmekioderma rea</i>	18			8					11	33	83
30	<i>Amphimedon erina</i>	18						8	5	22		100

environmental variables are displayed as arrows, indicating the direction of average increase of each variable, whereas categorical variables are

displayed as points (indicating the center of the occurrence of each category). The scores on the axis represent relative distance units in the

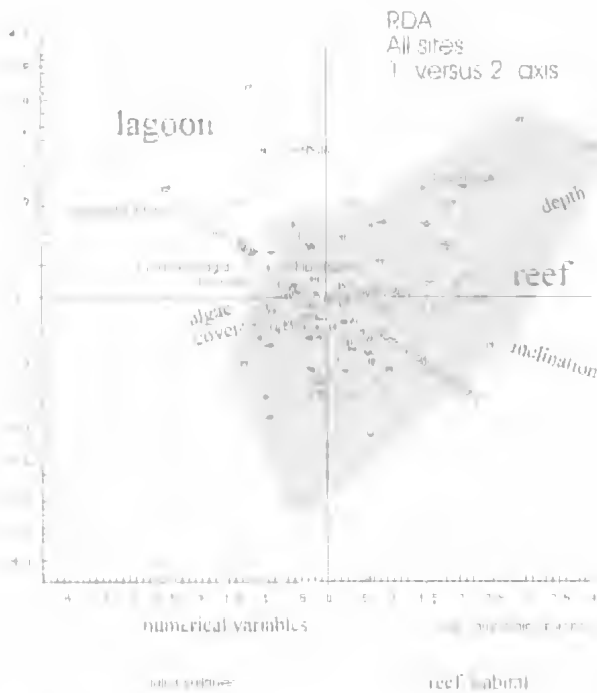


FIG. 1. Redundancy Analysis (RDA) of all sites. Similarity of sites is displayed as distance. Lagoonal and reef sites are differentiated on the first two axes with lagoonal sites on the upper left and reef-sites with grey background. Note that there is a mixing zone between lagoonal and reef-sites, indicating sites influenced by both environments. Numerical variables are shown as arrows. Differences in sizes of arrows reflect different influence of environmental variables. Ordinal variables are printed as centroids without direction but influence sites nearby. Numbers refer to site-numbers.

similarity matrix from the center of the data set. The following environmental variables were used in these analysis: Depth, size of site, total cover, sponge cover, coral cover, algae cover, inclination of substrate, ridges with freshwater outflow, *Thalassia* seagrass, backreef, bluchole, ship channel, fore-reef, deep fore-reef, pinnacle, undersides of platy corals, reef-flat, Discovery Bay, Rio Bueno, Pear Tree River, sediment cover, coral rubble.

An *a priori* selection of environmental variables was carried out. Only variables with $p < 0.05$ were retained for further analysis, to ensure that only statistically significant variables influenced the analysis.

RESULTS

COMPARISON BETWEEN SHALLOW WATER (0-40M) AND DEEP FORE-REEF (60-107M) SPONGES. The relatively well known Jamaican shallow-water sponge fauna consists of now 157 sponge species (Lehnert & Van Soest, 1998). 133 species (85%) are restricted to shallow water, 5 of them were new to science, and 24 species (15%) also occur in the deep fore-reef. From the deep fore-reef 60 sponge species were collected from 13 trimix dives. 23 of these are new (Lehnert & Van Soest, 1996, in press), and with 13 known species a total of 36 species (60%) are restricted to the deep fore-reef, 24 species (40%) are shared with shallow water habitats. The inventory of deep fore-reef sponges is far from being complete, with additional undescribed and described species expected. However, there are striking differences in species composition between deep water and shallow water habitats, and it is improbable that any additional deep fore-reef species will be found in the well known shallow water fauna.

INTERNAL ANALYSIS OF THE SHALLOW WATER DATA SUBSETS.

Classification. Table 2 shows the results of the classification obtained by the analysis outlined in Table 1, indicating ten groups of sites attributed to three large-scale habitats. Site-groups 3 & 4 are from undersides of platy corals with the characteristic species-groups 10 & 16. Lagoonal environments are represented by site-groups 1, 2, 9 & 10.

Characteristic lagoonal species include species-groups 14 & 18, restricted to lagoonal environments. Many species frequently occur within the lagoon, but have their focal points within reef-environments, like species-groups 1, 2, 3, 6, 11 and 12. The remaining site-groups 5, 6, 7 and 8 are from different reef-environments. Species-group 6 is most abundant in general reef environments. Consequently these species can be used for large scale characterization of habitats only, but not for subhabitats.

Ordination analysis using RDA was performed on a square-root transformation of the percentage substrate cover values, with centered and normalized species. The following environmental variables were statistically significant ($p < 0.05$): Depth, algae cover, inclination of substrate, ridges with freshwater outflow, *Thalassia* seagrass,

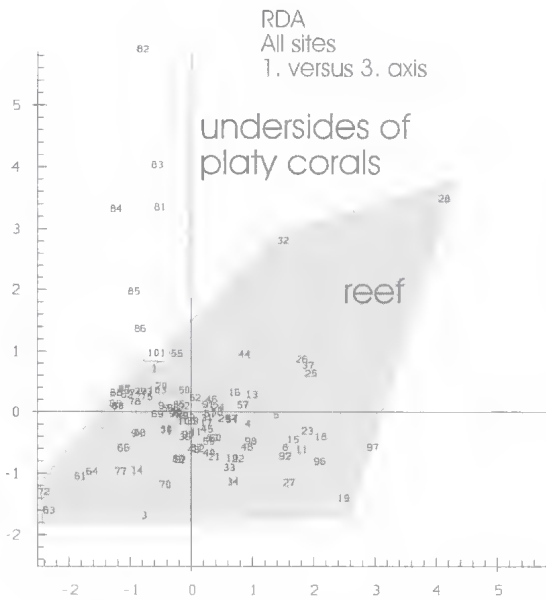


FIG. 2. Redundancy Analysis (RDA) of all sites. Representation of first and third axes show that undersides of platy corals is a valid large scale habitat distinguished in the third dimension. Numbers refer to site-numbers.

back-reef, Bluehole, Ship-channel, fore-reef, deep fore-reef, pinnacle, undersides of platy corals, Discovery Bay, coral rubble.

A plot of sites of the first two axes (Fig. 1) shows two distinct faunistic groups. Group 1 contains all sites from lagoonal environments, whereas group 2 contains sites from reef habitats. Sites and species are printed as numbers. For species names consult Table 2.

Looking at the third dimension of the sites plot (Fig. 2) a third group of sites is clearly separated from other habitats. All sites included in this group derive from undersides of platy corals where a completely different assemblage of sponge species occurs (Table 2, species groups 10 & 16). The lagoonal and reef-surface habitats were analyzed separately, whereas too few members of the 'undersides of platy corals group' excluded it from further investigation.

Reef surface. Excluding sites from the lagoon and the undersides of platy corals, the remaining sites from reef surfaces show a more-or-less continuous

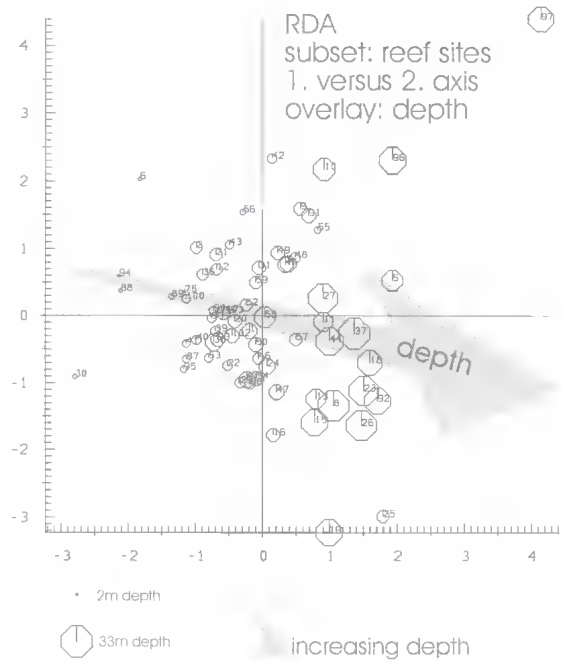


FIG. 3. Redundancy Analysis (RDA) displaying only reef sites. No distinct site-groups are recognizable, but depth as overlay (larger symbols indicate greater depth) shows arrangement of the sites along a depth gradient. Grey arrow indicates general direction of depth gradient (increasing depth from upper left to lower right). Numbers refer to site-numbers.

distribution along a gradient increasing depth, from the upper left to the lower right (Fig. 3). The sample areas 28, 32, 33 and 34 did not fit into this gradient, and have in common that they derive from reefs near river mouths. The location 'river mouth' is obviously different from other reef localities and therefore, these sites were omitted from further analysis. This area may be greater influenced by freshwater, sediments and turbid water although this is speculative and based on few sites only. Figure 4 shows the reef surface sites with substrate inclination overlayed, with an increasing trend towards inclination to the right indicated. The corresponding plot of the species (Fig. 5) shows preferences for species with regard to water depth and inclination. (e.g. species on the upper left are from more horizontal, shallow environments, whereas species on the lower right are from more vertical, deep environments). The two striking gradients, depth and inclination, have more-or-less the same direction, they are not

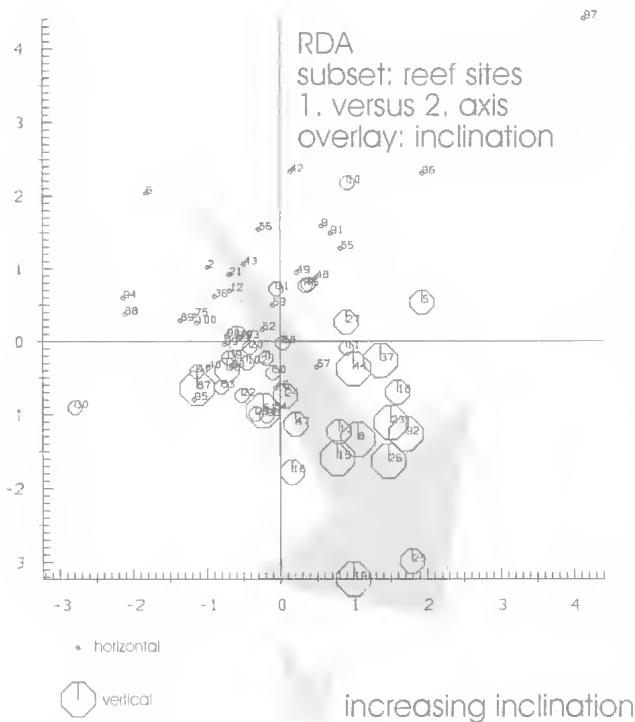


FIG. 4. Redundancy Analysis (RDA) of reef sites, with inclination of substrate as overlay. Larger symbols indicate greater inclination. No site-groups can be recognized, but a continuous arrangement of sites along a gradient of inclination from horizontal sites (upper left) to vertical (lower right). Grey arrow indicates general direction of increasing inclination. Numbers refer to site-numbers.

independent variables. There is undoubtedly an increase in steeper habitats with increasing depth, especially at the deep fore-reef. In these deeper waters there is a steep wall extending down to several hundred meters. However, depth alone is not sufficient to explain species' distributions because less inclined deep water habitats are settled by different species than more inclined deep water habitats. These two gradients do not produce clearly separated groups but the sites appear to be arranged along continuous gradients.

Lagoon. The separation of lagoonal sample areas from reef sites is shown in Figure 1. Inside Discovery Bay several subhabitats are evident. In shallow parts of the lagoon, close to the coast, many ridges occur where freshwater flows out. Two 'blue holes' are the deepest parts of the lagoon (13m and 50m), with very turbid water, fine sediments on the sea bed and probably also

some freshwater outflow. Extensive *Thalassia* seagrass-beds occur here and the eastern part of the bay is protected by land and reef from NE trade winds. Site-groups 1, 2, 9 and 10 (Table 2) are mainly from lagoonal environments. The site-groups 9 and 10 of the classification (Table 2) deviate somewhat from the results of the ordination (Fig. 6) whereby there is mixing between some sites from shallow fore-reef habitats with sites from the lagoon. This is probably due to recent hurricane destructions in which the topography of seaward lagoonal-, reef flat- and shallow fore-reef -habitats were more or less equalized, and therefore subsequently settled by similar species. For site-groups 1 (*Thalassia* seagrass) and 2 (freshwater ridges) classification and ordination analyses are in complete agreement. According to the ordination analysis of the lagoon subset (RDA, square root transformation, species normalized and centered), five groups of sites (a-d) are distinguishable and shown in Figure 6.

1) Blue hole: the sites 77, 78, 79, 80, 50 and 3 (site group 10) are from the large blue hole (the smaller blue hole mostly consists of bare sediments, and only a small part at the SE end is overgrown by sessile organisms). Sites 77-80 are from NE to W parts of the blue hole where seawater streams into the bay from the ship-channel. Clearly separated from these are sites 3 and 50 which are from the SE slope of the blue hole, locally known as the 'Columbus Park' locality. Here, influences of freshwater and pollution with bauxite are probable, the latter because of the proximity of the docking area of bauxite freightships. The remaining sample areas from group 10 are from shallow fore-reef habitats, as mentioned above.

2) *Thalassia* seagrass-beds: Very close to the 'blue hole' group is a group of sites from *Thalassia* seagrass-beds. The long leaves of the *Thalassia* seagrass slow down water velocity and lead to higher sedimentation comparable to the situation within the blue hole, and this is the most probable explanation for its statistical similarity to the 'blue hole' group. *Thalassia* seagrass often grows within the back-reef, and the seaward margin of the blue hole is also proximate to back-reef environments, so that these two habitats are not clearly differentiated in their faunistic composition.

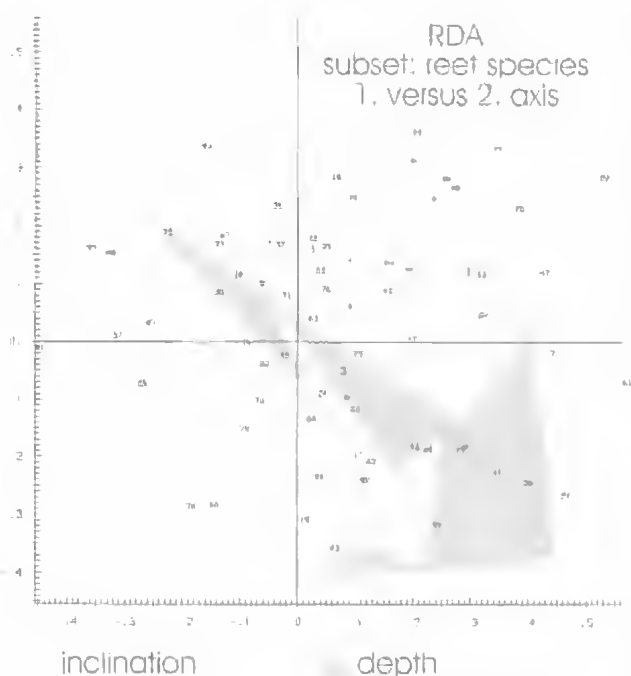


FIG. 5. Redundancy Analysis (RDA) of reef sites, showing a complementary plot of species data from Figures 3-4. Within reef habitats there are no distinct groups of species but species are continuously arranged along gradients. Upper left: shallow reef-species; center: species from intermediate depths or with indistinct depth distribution; lower right: deep reef-species. Numbers refer to species numbers in Table 2.

3) Ridges with freshwater outflow: (group 1, Table 2). These ridges are often surrounded by *Thalassia* seagrass-beds but the influences of the freshwater are strong enough to promote settlement of a different fauna here.

4) Protected back-reef: Clearly separated from other lagoonal environments are two sites from the eastern back-reef. This environment is very close to the blue hole. Consequently, the water here is more turbid than in western parts of the reef. Furthermore, the eastern back-reef is in lee of prevailing waves from the NE trade winds.

DISCUSSION

Hechtel (1965) investigated only 10 (sometimes very small) localities on the south coast and one cannot be sure that individual random differences are responsible for the observed distributions. Because there are considerable differences in sponge species along the north coast, a direct

comparison between Hechtel's and our results is not appropriate.

Alcolado (1990) differentiated reef-sponge communities, which he subdivides into less than 10m depth and 10-30m depth, mangrove-sponge communities, macrolagoons and bathyal-sponge communities (150-608m depth). He described the common species in each community and compared diversities, but obviously chose depth-classes before sampling. Alvarez et al. (1990) also focused on the importance of depth gradients in influencing species distributions, and found that there were "a few abundant species and many uncommon ones... The most frequent species are also the most widely distributed along the depth gradient." They also conclude that "For all species, the values of density and area coverage varies along the transects but seems independent from depth". These data seem to contradict our results. But their investigation obviously focuses on the few abundant and dominant species, whereas our results are based on the analysis of the whole species composition with a data transformation avoiding dominance types.

Diaz et al. (1990) also studied community structure of sponges along depth gradients. They compared species number, area coverage, density, diversity and evenness. Again, in contradiction to our results, they found that "The results of the cluster analysis confirm that the sponges in the study area lack a well defined pattern of zonation", and the "predominance of encrusting species at almost all depths". However, in looking for differences between transects they restricted their question to zonation based on depth alone. Schnahl (1990) investigated the distribution and abundance of sponges in southern Florida reefs at three depth zones and found that "distributional patterns of sponges may be used to identify the ecological factors that influence the communities in this area".

Whereas all these investigations focused on depth zonation only and comparing pre-defined regions of the reef, the present paper makes *no a priori* assumptions about reef zonation, irrespective of bathymetric or habitat bias, instead using subsets of sites with similar species composition, provided by multivariate analysis.

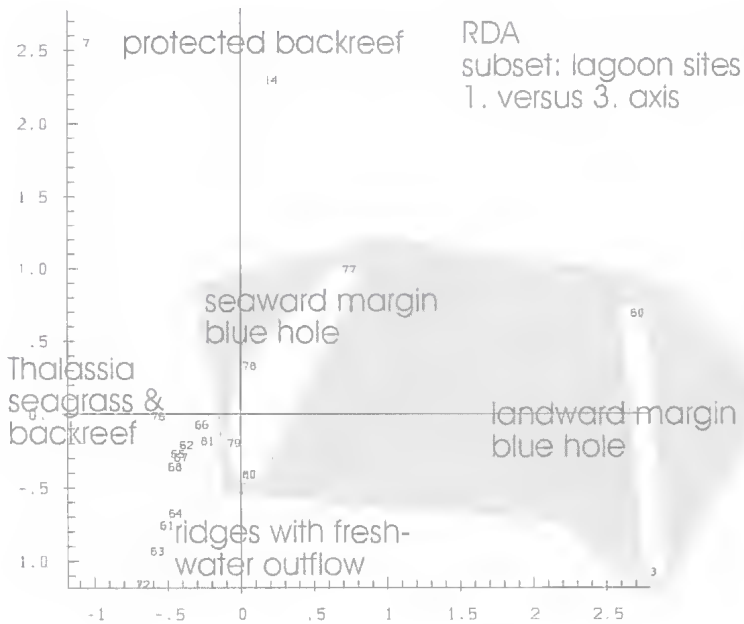


FIG. 6. Redundancy Analysis (RDA) of lagoon sites. Several groups are distinguished, characterising different subhabitats, however, small sample sizes of group-members weakens the interpretation. Numbers refer to site numbers.

Only then we began interpretation of these groups of sites with field data.

The analyses made are objective and repeatable, but we have to admit, that for our conclusions there is no objective test. We think the conclusions are well justified because in most cases there are enough members of the group, making our conclusions probable. Exceptions are the subhabitats within the lagoon. The groups have only few members and we are aware of the risks of interpreting natural variation. But the groups are easily explainable and fit very well in environmental differences, observed during dives, that we think it worth, to include them here.

COMPARISON WITH GOREAU'S ZONATION OF JAMAICAN CORAL REEFS. Goreau (1959) described a reef near Ocho Rios, N Jamaica, 34 year ago, in relatively close proximity to Discovery Bay. He claimed the Ocho Rios reef to be "typical of the large fringing barrier reef communities found along the north coast of Jamaica." and was also familiar with the Discovery Bay reefs. Furthermore, Goreau & Wells (1967) wrote "... that extensive surveys carried out in other parts of Jamaica over more

than 10 years have shown that the Discovery Bay reefs are representative for the island as a whole...". Consequently we believe that comparison between their results and ours is well justified. Goreau made a more intuitive approach, naming zones either after dominant species or after striking morphological structures, while in the present paper we tried to find characteristic species from different habitats (which need not to be dominant) and their correlations to some abiotic factors. We consider it is worthwhile comparing these results to see what is still recognizable and what has changed.

Goreau distinguished three regions, back-reef, reef-crest and fore-reef, which were also divided into 7-9 different zones. These are considered separately below with remarks as to the present status of these reefs and

differences between these two data sets.

1) Goreau divided the back-reef region into a shore zone, with a variety of hermatypic corals, and a lagoon zone, with less corals. The shore zone has almost disappeared. Now, only one small protected area within Discovery Bay has living corals close to shore. *Acropora palmata* has disappeared, *Millepora complanata* dominates this small spot. The upper parts of this 'inshore reef' is now dominated by the green zoanthid *Zoanthus sociatus*, a species which is described by Goreau for the reef flat (which he called also the *Zoanthus* zone), but where it is barely present today. Additional to Goreau's zones the present paper distinguishes four lagoonal subhabitats (blue hole, *Thalassia* seagrass-beds, ridges with freshwater outflow and protected back-reef) separated on the basis of faunistic data. Obviously Goreau worked on a larger scale. Goreau's 'inshore reefs' were probably destroyed by the hurricanes, and he did not divide the lagoon-zone into subhabitats.

2) Goreau's reef-crest region is divided into rear-zone, reef-flat (zoanthus-zone), palmata-

zone (with breaker and lower palmata zone), and buttress-zone. Probably, again due to hurricane destruction, it is now not possible to recognize all of these zones. Rudiments of his rear-zone can be recognized in some parts, with still large *Montastrea annularis*, *Diploria strigosa* and *Siderastrea siderea*. The reef-flat or zoanthus-zone has changed very much. *Zoanthus sociatus* can only barely be found. There are still some *Millepora*, but *Gorgonia* and *Lithothamnium* are rare. Large dead coral rocks, often above sea-level, occur instead. On the sides of coral rocks some small *Solenastrea* sp. occur. His palmata-zone also does not exist any more, replaced by hargrounds, settled by the sponges *Anthosigmella varians* and *Chondrilla nucula*. The previously dominant *Acropora palmata* exists only with some scattered (sometimes large) colonies. The buttress-zone can still be easily identified but, the sediment canals, described by Goreau as "...very narrow, somewhat winding, canyons the walls of which are perpendicular or even overhanging" are now wide sediment streams, the walls less inclined. Exceptions are found in front of the mouths of the Rio Bueno and the Pear Tree River, where some buttresses come close to Goreau's description. However, these localities seem to have suffered less destruction than any other reefs investigated. Another striking difference are the depths given by Goreau. He wrote: "At the buttress crests, the depth averages only about 2 meters whereas the canyons are between 8 and 10 meters deep." Now the buttress crests range between 5-20m depth and the sediment areas between 7-23m. The uppermost region of the buttresses has probably been destroyed or buried and considerable amounts of the buttresses have been removed. This seems very probable because Goreau described *Acropora palmata* on top of the buttresses where they no longer exist, even as dead colonies. While Goreau stated the cover of living coral was 90% of the available surface, it is now about 15%, except for a few small areas at the walls of the buttresses where 90% coral cover occurs.

3) The seaward slope or fore-reef was divided by Goreau into the cervicornis-zone and the annularis-zone. Both zones have completely disappeared. He located the cervicornis-zone at 'the uppermost region of the seaward slope', seaward of the buttress-zone. Now there are large sandy areas between the buttress zone and the shelf break. *Acropora cervicornis* is now found only sporadically in the buttresses. At the shelf

break there are some pinnacles, the edge, and wall of the break itself below 30m depth, covered with numerous large *Montastrea annularis*. This area is much deeper than Goreau described as the annularis-zone, where he gave an average depth of 15m. The 'undersides of platy corals-habitat' described here was not mentioned by Goreau, probably because he did not investigate these depths and he was also mainly interested in hermatypic corals. This habitat is a very small component of the 'area scale' used by Goreau, although relatively large from our faunistic approach. Some differences between our results and those of Goreau are related to our different approaches and methodologies (e.g. our lagoon subhabitats, or the undersides of platy coral habitat). Other differences, like the missing palmata zone, cervicornis-zone or the different depths of the buttress zone seem to be due to destruction by hurricanes.

To summarize the changes since Goreau's investigations published in 1959, it is obvious that the fringing reefs with three distinguishable main structures (back-reef, reef crest and fore-reef) have changed into a situation where the back-reef has lost its inshore reefs and has gradually merged into a long seaward slope with nearly no living reef crest in between. Goreau's internal zonation of reef crest and seaward slope can now only be recognized in parts while several striking structures described by him have completely disappeared. Extensive growth of algae seems to inhibit recovery of the reefs.

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